

5.

Army-ant Life and Behavior under Dry-season Conditions
with Special Reference to Reproductive Functions.

II. The Appearance and Fate of the Males.

T. C. SCHNEIRLA.

*The American Museum of Natural History.*¹

(Plate I; Text-figure 1).

INTRODUCTION.

In keeping with the marked deviations of the doryline ants from most other ants in their general behavior pattern, there are extensive differences in their mode of reproduction. The close relationship which exists between general reproductive pattern and colony behavior in the American subgenus *Eciton* (*Eciton*), has been described in previous reports (Schneirla, 1938, 1944). The present paper represents an attempt to throw further light upon *Eciton* reproductive processes by inquiring into dry-season events and particularly the appearance and function of *Eciton* males.

The wasplike winged males of the dorylines, which contrast sharply with the curiously-structured wingless dichthadiigynes or fertile females of these ants, have been described by various authors (Gallardo, 1920; Mukerji, 1926; Wheeler, 1921; Smith, 1942), yet the manner in which these reproductive forms are produced and the nature of their functional relationship to colony activities have remained obscure to the present time.

The elusiveness of this problem is suggested by my failure to find any trace of developing *Eciton* male forms during the rainy season, notwithstanding the fact that an extensive search of the nests was carried out in the rainy months of four different years. The studies (Schneirla, 1933, 1938, 1944) were made in the Caribbean area of Panama, in a region that has well marked and fairly regular annual rainy and dry seasons. It would seem by elimination that young reproductive individuals of both sexes must appear during the latter part of the rainy season or in the course of the annual dry season.

Most of our previous evidence on the fertile forms of *Eciton* has come as we shall see (in the "Discussion" section of the present paper) from the occasional capture of males and females in scattered localities, under seasonal and colony conditions which are generally very incompletely reported.

The desirable procedure to clarify the confusion is a comparison of data from areas with similar annual climatic changes. A beginning was made by the writer in the dry season of 1945, in a sampling of *Eciton* colonies in various rain-forest localities in southern Mexico through the latter two-thirds of the regular dry season (Schneirla, 1947). This general area was selected because its annual rainy-dry seasonal cycle approximates that of the Atlantic rain-forest area of Panama. In that study various well-separated localities were visited successively, a procedure calculated to give a broad view of *Eciton* conditions through the period. A predominance of worker broods was found, with but limited evidence on the reproductive forms. Just one brood of developing males was found, under conditions somewhat resembling the single male brood previously found by Wheeler (1921). It is clear that a cross-sectional survey is not adequate for the study of events as elusive as the production of *Eciton* fertile forms appears to be.

The present survey represents a longitudinal or relatively continuous survey of conditions in the locality of the original Panama studies. As was anticipated, male forms appeared in the *Eciton* broods and an extensive study of their relations to the colonies became possible. Among the questions to which the study was directed were these: Do the males appear in distinctive broods or in mixed broods (e. g., with worker forms)?—How many males may be produced by a given colony, and do all colonies produce them?—Is the production of males synchronized in some manner with the ordinary production of worker broods by *Ecitons*, or does this process occasion interruptions or irregularities in the ordinary reproductive rhythm? Such questions are of interest not only from the standpoint of *Eciton* reproductive functions, but also with regard to the general problem of caste determination in insects.

We are of course interested in learning the relationships of males to colony behavior, both when they are in broods and after they have emerged as alate adults. We have found that worker broods have a regular and important causal function in the occurrence of the periodic nomadic and statary changes in colony behavior which are consistent

¹ This investigation was carried out while the writer was a Fellow of the John Simon Guggenheim Memorial Foundation. Supplementary studies have been supported by a grant to the Department of Animal Behavior from the Committee for Research in Problems of Sex, National Research Council.

features of *Eciton* life under rainy-season conditions (Schneirla, 1938; 1944). Is it possible that the appearance of developmental forms other than workers is reflected in a different set of relationships between brood and colony?

Finally there is a whole set of questions concerning the behavior and function of the males, in particular the conditions of their dispersal as winged individuals and the manner of their eventual meeting with the unique wingless *Eciton* dichthadiigynes. Problems such as the last, concerning the process of mating, will be touched upon only circumstantially here in relation to the dispersion of the males from their colonies of origin.

LOCALITY AND GENERAL CONDITIONS OF THE INVESTIGATION.

This paper is based upon a systematic investigation of *Eciton* behavior and related colony conditions in a given general locality, Barro Colorado Island, C. Z., through the principal part of a given dry season.

The survey extended over roughly the last three-fourths of the dry season of 1946 into the early part of the next rainy season, in all from February 7, 1946 to June 16, 1946. Until near the end of this period rains were exceptional and generally very light, with numerous sequences of rainless days until after mid-April. These circumstances are typical of the locality.

That there is a sharp seasonal difference in rainfall on Barro Colorado Island (as in the Caribbean area generally) is clear from the fact that in a summary of monthly averages and deviations for a period of fifteen years on the Island during which records were kept by the same method, the smallest monthly rainfall probable in the wet months from May through November (6.3 in. for September) clearly exceeds the largest monthly fall probable in the dry months from December through April (5.0 in. for April).² Thus the Island itself may be considered a very satisfactory region in which to investigate the seasonal differences in ecology and behavior of tropical American rain-forest animals. With respect to dry-season conditions in the spring of 1946, it should be added that the preceding wet season had brought an exceptionally large fall of rain before dry weather set in about mid-December; consequently even the rather high ground of Barro Colorado, well-forested as most of it is, may have retained more moisture than is usual during the dry season. Only the terrain in the eastern section of the Island, with its lighter forest cover than other sections, approached in dryness the conditions generally encountered in southern Mexico in the spring of 1945 (Schneirla, 1947, areas 1, 3 and 4).

The study is mainly concerned with two terrestrial species of the subgenus *Eciton*

(sensu stricto), which are among the most frequently encountered members of the genus *Eciton* in Central America.

The general method involved surveys of behavior and biological conditions of *Eciton* colonies in the field, with special field and laboratory tests introduced when feasible. The plan was to keep as complete a record as possible of army-ant colonies present in the eastern and southeastern half of the Island (the drier section). Two colonies, one of *Eciton* (*E.*) *burchelli* (colony B-I) and one of *E.* (*E.*) *hamatum* (colony H-B) were kept on record throughout the four months of the study, and numerous other colonies of these two species were studied for shorter intervals of time.

At intervals of about three days through the period of investigation, when accessible the bivouacs of colonies under observation were broken into as carefully as possible for brood samples. Periodically the bivouacs of colonies other than the two principal cases (B-I and H-B) were ransacked for a thorough inspection of their brood and adult population. A large part of the collected brood material was fixed in a modified Bouin's solution before preservation in 70% alcohol.

Live *Eciton* material was kept at the laboratory for special behavior observations and tests arising from the field work. For sampling the population of flying *Eciton* males, occasionally a small light trap was set at various places in the general forest and a larger light trap was placed in the forest near the laboratory clearing. Also, a white illuminated board just outside the main laboratory building was inspected each night for alate males.

RESULTS.

General Results: The Nature and Occurrence of Eciton Male Broods.

It has developed from numerous seasonal investigations on Barro Colorado Island (Schneirla, 1933, 1938) that in the regular season of rains in that locality *Eciton* colonies produce only worker forms in immense broods. No sexual forms were found in a great number of broods examined during the period from May through September. Our present results indicate that the production of males is seasonally conditioned, and evidently limited to the dry season.

The general findings are summarized chronologically in Table I. From the time the study was begun on February 7 until the latter part of February, only broods containing worker forms were found in the bivouacs of *Eciton burchelli* and *E. hamatum*. In agreement with the 1945 results from southern Mexico, such broods resembled those of the rainy season in containing the entire polymorphic series of worker types, and from general inspection seemed to approach them in numbers of individuals (ca. 25,000). The first brood containing male forms was found on February 16 in a colony of *E. burchelli* (No. B-III), chanced upon

² The writer is grateful to Mr. James Zetek, Resident Manager of the Barro Colorado Island laboratory, for having made this data available, and for the many other ways in which he generously facilitated arrangements for these investigations.

late in the evening during the early part of its bivouac-change movement. It was observed that some rather bulky larvae were being carried by workers in the column. Samples of these larvae were taken, and later at the laboratory were found to be all of the characteristic sub-cylindrical male type and all nearly the same size, about 14 mm. in length. On February 20, when the bivouac of this colony was examined carefully, the brood was estimated to contain 3,000 larvae, all of the male type and not very different in size. The last distinct brood of males found in the investigation was a lot of alate males discovered in a colony of *E. hamatum* (H-L) on April 16. As Table I indicates, male broods were discovered in various other colonies of both *E. burchelli* and *hamatum* during the intervening period of about two months.

Representative stages of development in *Eciton* males, from early larval to mature forms, are illustrated in Plate I.

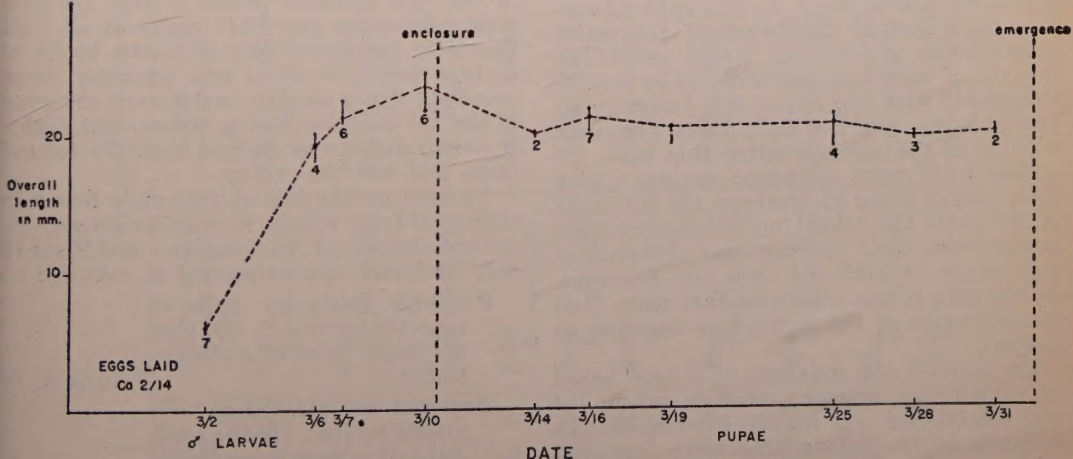
Altogether, male broods were found in 5 of 26 different colonies of *E. hamatum* under observation at different times from mid-February to late April, and in 6 of 21 different colonies of *E. burchelli*. Dealate males in limited numbers were found at intervals in the colonies of both species up to the time when the study ended in mid-June. In these species the production of males seems to be confined to the dry months.

The results summarized in Table I suggest that a species difference exists in the time of male-production. Inspection of the captures shows that male broods of *E. burchelli* were found from shortly after mid-February, when early larval broods were discovered in the bivouacs, to the end of March when only alate forms were found. In contrast, larval male broods of *E. hamatum* were not found until the middle of March, and alate broods of this species were not taken until mid-

April. Notwithstanding the relatively small number of cases, in view of the fact that numerous colonies of these two species were investigated with approximately equal frequency during the period, it is quite possible that we are dealing with a reliable difference in the timing of male production. Especially suggestive is the fact that all of the respective stages of *E. hamatum* males from early larvae to dealate forms were taken later than were the corresponding male types of *E. burchelli*. The *burchelli* colonies on the Island evidently begin their production of males earlier than do *hamatum* colonies, and finish earlier. Judging from the fact that winged males of various species of *Eciton* (*Labidus*) and *E. (Neivamyrmex)* were taken at lights from the early part of February, it is possible that males are produced still earlier in the season in some of these species.

In this study, two colonies of different species of *Eciton* (*Eciton*) were kept on record for approximately four months after early February. All of the principal activities such as raids and nomadic movements were investigated, and whenever possible samples of their broods were taken at 3-day intervals. In one of these colonies, H-B of *E. hamatum*, four all-worker broods were produced during the interval, but this colony produced no males of its own. Within the same time, colony B-I of *E. burchelli* brought forth three worker broods and in addition one all-male brood of its own. There follows a résumé of the latter case, which as various other results indicate is representative of the circumstances of male-production in species of *Eciton* (*Eciton*).

The record of colony B-I, *E. burchelli*. The colony was found on February 6, through chancing upon its raiding system. At the time its bivouac cluster was established within a large hollow tree, about 2.5 meters from the ground, one side of it visible



TEXT-FIG. 1. Sketch of representative stages in the development of a male brood of *E. burchelli* (colony B-I), from larva to mature pupa. Size at each stage is represented by the overall length of specimens taken in small samples. The number of individuals in each sample is indicated below the short vertical line representing range and average of lengths in the sample.

through a huge knothole. This was clearly a statary site into which the colony had moved within the preceding few days, for an immense brood of probably more than 25,000 mature worker larvae newly enclosed in cocoons was present. On February 16 unsuccessful attempts were made to discover and sample a new brood of eggs which, in the regular cycle of Eciton events, would be expected at about that time (Schneirla, 1944). On February 28, with the greater part of the now mature worker brood removed as callows from cocoons, the colony set off upon a nomadic period in which raids were larger than before and successive nightly bivouac-change movements occurred.

Larvae of the new brood, which later proved to be an all-male brood, were taken from the temporary bivouac of March 2. These larvae were all nearly the same size, about 6.4 mm. in length. In the following days they grew with surprising rapidity. For example, on March 10 a small sample of six of them approximated 23 mm. in length. At that time these larvae evidently were nearly mature, for the first spinning was observed on March 9. The growth rate of this brood is represented in Text-figure 1.

On March 10, when the colony spent its first day of a new statary period clustered within the basal trunk cavity of a large hollow tree, cocoon-spinning appeared to be widespread among the mature male larvae. The spinning evidently lasted about six days in all. On March 19 approximately 200 of the enclosed larvae were dragged by workers to the outer edge of the tree-opening, where they were discarded. All larvae in the heap of discards were found to be dead at the time. A general examination disclosed no clue as to possible causes of death.

On March 29, when all members of the male brood seemed to be nearly mature pupae in a well-pigmented condition, the colony began to shift away from its statary site in the hollow tree.³ At this time laboratory tests showed that most of the males were capable of antennal, tarsal, and trunk reflexes of sufficient amplitude to be readily observable with the naked eye. Large numbers of newly emerged alate males were seen nightly in the columns after this time, together with many unopened cocoons which were lugged along by workers. On the night of March 31 the "shucking" of mature male pupae from their cocoons was observed in full swing at both old and new bivouacs. At the time it was estimated that more than three-fourths of the males had emerged as callows.

On April 1 the presence of a new brood of very young worker larvae in colony B-I was established. The nightly bivouac-change columns of the colony now were thronged with many hundreds of alate males, passing

along the trails under their own power in single file or in small groups, generally surrounded and closely followed by workers in large groups. Successive nightly movements were observed in which for periods of two hours or more the alate males ran in column with workers from the old to the new bivouac site. The males appeared only during the nightly removals; in the daytime they remained within the bivouac cluster and never were seen among the workers on the raiding trails.

On April 2 the emergence of this brood from cocoons seemed to be complete. Judging by a count of empty cases collected from the statary site and first few nomadic bivouacs, this brood of males numbered close to 3,000 individuals.

Each evening after April 3, within a few hours after dusk in the early beginning of the bivouac-change, as many as a few dozen winged males were to be seen in the vicinity of the bivouac of the day, running circuitously about on the ground and on low vegetation and other objects close to the ground. Generally each male had a few workers hanging to his body or running in close contact with thorax or gaster. No departure flights were observed until after April 5, then on succeeding nights the male take-off flights were observed frequently, from the vicinity of the old bivouac and sometimes from the new site, but never from the moving column. (No movements of the colony occurred on the nights of April 4, 6, and 8.)

On April 14, when colony B-I entered a further statary period (with its larval worker brood now mature and engaged in spinning), alate males were not very numerous, and it was judged that not more than 600 of them remained with the colony. A few nightly departures of males were observed during the statary period, from the large lightning-split tree in which the colony was clustered, until in the first bivouac-change movement of the new nomadic period it was not possible to observe any alate males at all. (At this time the major part of a new brood of mature pupal workers had emerged from cocoons.) Since no alate males were observed in the B-I columns during subsequent nightly removals, it was judged that the last of them had left the colony.

To sum up the life of this male brood in colony B-I in which it was produced, its growth stages (cf. Text-figure 1 and Plate I) may be timed approximately as follows:

Probable midpoint date of egg-production: (During the early third of a statary phase). February 14

Presence ascertained as very young larvae: (In the early days of a new nomadic period). March 3

Mature male larvae at height of cocoon-spinning: (At beginning of a further statary period). March 10

³ The nightly bivouac-change movements through which this colony shifted from the statary site of March 10-31 were complex and rather exceptional, involving as they did a process of true colony-division which will be discussed in a forthcoming paper.

TABLE I.
Principal records of male Eciton broods in the 1946 dry season at Barro Colorado Island.

Date found	Colony symbol and species	Condition of male brood	Estimated brood population	Other broods present	Colony behavior	Remarks
Feb. 22	B-II-X <i>E. burchelli</i>	Nearly mature larvae	3,000	Large brood of callow workers	Nomadic; four nightly moves observed	No movement on second night after large part of male brood was taken away
Mar. 1	B-III <i>E. burchelli</i>	Mature pupae, largely emerged alates	3,000	Large brood very young worker larvae	Newly nomadic; three successive nightly moves observed	Evidently found on day following the first nomadic move
Mar. 2	B-I <i>E. burchelli</i>	In early larval stage	3,000	Large brood newly emerged callow workers	Nomadic; on move until larvae mature, enclosed	Nomadic activity rose considerably in following days
Mar. 6	B-IV <i>E. burchelli</i>	Adult alates	500	Large brood nearly mature larval workers	Nomadic; four successive moves, then statary	No males remained after statary period of 22 days
Mar. 29	B-V <i>E. burchelli</i>	Adult alates	1,000	Large brood fairly mature larval workers	Nomadic; two successive moves observed	Exodus of males observed from bivouac area
Mar. 31	B-VI <i>E. burchelli</i>	Adult males	500+	Large brood mature larval workers	Nomadic; moved that night into statary bivouac	No alate males remained after statary period of 21 days
April 3	H-J <i>E. hamatum</i>	Very young larvae	3,000	Large brood newly emerged callow workers	Nomadic; large raids, two successive moves seen	Just three days after statary period
April 4	H-K <i>E. hamatum</i>	Larvae more than two-thirds grown	3,000	No other broods observed	Nomadic; two successive moves observed	Raids exceptionally large; movements long
April 9	H-L <i>E. hamatum</i>	Newly emerged callow alates	2,000	Large brood very young worker larvae	Nomadic	Queen contracted; two de-alated males found in bivouac
April 10	H-M <i>E. hamatum</i>	Newly emerged callow alates	2,000	Immense brood very young worker larvae	Nomadic	250 meters from H-L; possibly from same base colony

Mature males emerging from cocoons: (At beginning of a new nomadic phase). March 31
 Alate males probably all gone about April 20

Provided that the eggs of this brood were laid on or about February 14, as there is reason to believe was the case, the total development time of this male brood was close to 46 days, with 22 days of this time for growth from the stage of larval maturation to pupal maturation. The males left the colony in nightly lots, and practically all of them appeared to have flown off within little more than three weeks from the time of their emergence as callow alates. Actually, the major part of this brood got away during the nomadic period of about 12 days which followed directly upon their emergence from cocoons. However, no departure flights were witnessed on the first three nights after emergence from cocoons had begun.

Colony B-I had but one brood of males, preceded by one immense all-worker brood and followed by two others, all broods appearing at regular intervals during the period of study. The total developmental time of the male brood was roughly the same as that of worker broods.

Evidence from briefer studies of male production. In all, 11 male broods were found in 47 colonies of *E. burchelli* and *E. hamatum* studied during the season of investigation. The chief characteristics noted above in the evidence from the production of a male brood by colony B-I were confirmed in briefer investigations of the other cases. The gist of the evidence from the other ten cases is presented in Table I, in chronological order, and further relevant facts from other colonies are given below, roughly in the sequence of developmental stages.

Colony H-J (*E. hamatum*) was found at 11:00 a. m. on April 3, engaged in a large three-system raid from a temporary bivouac 100 meters to the east of the Shannon trail, opposite Station 6.⁴ There was a brood of many thousands of newly emerged callow workers, relatively few of which were to be seen outside the bivouac. Near the rear center of the cylindrical bivouac cluster were found two walnut-sized clumps which contained relatively small sub-cylindrical larvae (later identified as Eciton male larvae) all roughly the same size. The colony was definitely nomadic, since it moved to a new bivouac site late that evening, and staged a new 3-system raid on April 4. Two broods: a large brood of callow workers, and a brood of young male larvae.

Colony H-K (*E. hamatum*) was found at 10:00 a. m. on April 4, about 200 meters to the east of Wheeler trail near station 22. A large 3-system raid was in progress; the bivouac was a very broad irregular cylinder beneath a large log. Well distributed through

the walls and interior of the mass was brood of male larvae considerably more mature than the brood of colony H-J, and estimated to number between 2,500 and 3,500 individuals. That evening the colony moved to a new bivouac site about 200 meters distant. One brood: a relatively small brood of moderately developed male larvae.

Colony B-II-X (*E. burchelli*) was found the move into Lutz ravine on the evening of February 20, crossing Barbour trail near station 2. In the column were observed many thousands of newly emerged callow workers distinguished from older workers by their light pigmentation, and large numbers of rather advanced male larvae lugged along by workers. The bivouac of February 21 could not be investigated; however the move of that evening was traced to the new site, and on February 22 the bivouac contents were examined. The brood of callow workers was relatively immense; that of male larvae was much smaller and was close to maturity. The new bivouac of February 23 was an unusually tall structure. It was a regular cylinder 90-100 cm. in height and about 35 cm. in width at the top (depending to the ground from the undercut upper edge of a broad buttressed root) and tapering inward toward the bottom which touched the ground. The male larvae were evenly distributed throughout the walls of the cluster, held by workers, and heaped in occasional pockets in the interior meshwork of workers. Nightly moves were observed until February 25 when the colony held its position within the base of a small partially open hollow tree, occupied the night of February 24. Late in the day on February 25 signs of larval cocoon-spinning were observed. On the night of February 26, after a very large raid during the day, the colony moved across Donat trail beyond station 3, about 160 meters to the north where a cluster was formed against the upper interior wall of a great hollow tree. Cocoon-spinning by larvae was greatest on February 27, judging by the rate at which wood dust fell to the ground from the elevated cluster of ants, and by the same sign this activity was completed on February 29 (as far as transportation of larvae to spinning places by workers was concerned). On the evening of March 21 the colony moved away, leaving a large heap estimated to contain more than 2,000 male pupa cases on the tree floor. Two broods: one immense brood of callow workers, one relatively small brood of males. Presumably a further brood of eggs was laid early in the 22-day stater period.

Colony B-III (*E. burchelli*) was discovered at 8:30 a. m. on March 1, about 300 meters to the north of the Van Tyne trail near station 8. At the time the last ants were leaving in column from what was evidently the previous bivouac site of the colony beneath the overhung side of a somewhat raised log, found under the log in one spot was found a sizeable heap of empty male pupa cases. (These were later counted at the laboratory, and

⁴ See special map of Barro Colorado Island prepared by 11th Engineers, Office of Department Engineer, Panama Canal Department U. S. Army.

talled 2,740). The column itself was ringed with alate males, and other alates were huddled in small groups at occasional places along the route where workers were seen with small numbers of male cocoons, some in the process of being opened. The alate males were strung out at intervals in the column, each running with an entourage of workers. The new bivouac was about 100 meters distant from the log under which the previous site evidently had been, and was a large exposed cylinder depending from low vines to the ground. The alate males remained within this cluster once they entered. The bivouac was found to contain several hundreds of alates, more than 100 unopened and partially opened male cocoons, and an immense brood of very young worker larvae gathered into a few masses in the very center of the bivouac. The described column evidently took the route of a protracted bivouac-change movement which had lasted through the preceding night. This route was not used after the movement was completed at 9:25 a. m. During the day a vigorous raid developed southward, and that night the colony moved to a new site over the principal trail of this raiding system. Further raids and bivouac-change movements were observed on March 2 and 3. The last male cocoons were opened on March 3. Two broods: a newly merged brood of callow alate males estimated to number about 3,500; and an immense worker brood in the early larval stage at the time of study. With the appearance of the callow males the colony clearly had terminated a statary period at the time it was discovered.

Colony B-V (*E. burchelli*) was found at 1:40 a. m. on March 29 on Ocelot Hill about 50 meters to the southeast of station 8 on the Shannon trail. The colony formed an elongated cluster wrapped around the trunk of a small tree, its bottom clearing the ground by about one meter. The ants were staging a large raid. Distributed through the bivouac walls and interior was a brood of alate males estimated to contain not more than 1,000 individuals, and an immense brood of nearly mature worker larvae. That evening the colony moved about 150 meters to occupy a site in the upper interior of a small hollow tree. On the following day the ants staged a large raid, but their bivouac-change movement that night had to go unobserved and the colony "escaped." Since some spinning had been observed in the essentially mature larval worker brood, it is probable that the colony became statary on March 30 or 31. Two broods: a brood of alate males, evidently reduced to a few hundred by previous departures, and an immense brood of nearly mature larval workers. The colony was nomadic, but evidently about to enter a statary phase.

Colony H-L (*E. hamatum*) was found at 1:40 a. m. on April 9, bivouacked about 50 meters to the south of the cut-off trail between Wheeler 14 and Armour 3. A large 3-system raid was in progress. The bivouac,

a cylindrical cluster formed against a buttressed tree root, contained many hundreds of recently emerged alate males (but no male cocoons), and an immense brood of very young worker larvae massed in a few boluses in the very center of the cluster of ants. (The queen was found in the contracted condition; also, two dealated males were discovered in the cluster.) The colony did not move that night (possibly because of my having thoroughly disrupted the bivouac); however, after a large 3-system raid on April 10, a bivouac-change movement over more than 250 meters occurred in the evening. The colony evidently was in the early stages of a nomadic period. Two broods: a newly emerged brood of callow alate males estimated at 2,000 individuals, and an immense brood of very young worker larvae.

Colony H-M (*E. hamatum*) was discovered at 10:00 a. m. on April 10 about 75 meters to the north of Armour 2. A large 3-system raid was in progress, distinctly separated from the raiding system of colony H-L. In the bivouac, an irregular mass under low vines, there were found hundreds of alate males and a brood of many thousands of very young worker larvae. Despite the separation of raiding trails, this colony and H-L may have been divided from the same colony within the days just preceding, a possibility supported by the similar status of their two broods and by their presence in the same area. Two broods: hundreds of alate males, and a large brood of very young worker larvae.

Colony B-IV (*E. burchelli*) was found on March 6 at 10:15 a. m., bivouacked 150 meters southeast of Barbour 3, and raiding vigorously to the northward. The large irregular bivouac cluster, massed beneath some vines, contained hundreds of alate males and a huge brood of half-matured worker larvae. On each of the following days until March 11 this colony carried out large daily raids and successive nightly movements. On the night of March 8 one dealated male was seen in the bivouac-change column, moving along under his own power closely followed by groups of workers. In each of the nightly movements the column was crowded with alate males, and numerous males were observed in take-off flights from the vicinity of the bivouac. On the night of March 11 a dealated male was seen in the column within a few meters of the old bivouac, running toward the cluster with numerous workers clinging to his gaster. On the night of March 12, when the colony moved into a hollow tree near Wheeler 2, which was to be its statary bivouac for the next 21 days, it was estimated that perhaps 300 alate males remained. (At that time the mature larval worker brood was spinning cocoons.) On March 22, when the colony was etherized and the bivouac ransacked (to check the time of egg-laying in the queen) no winged males were seen. On April 1 the first signs of cocoon-opening were noted, and on the evening of April 3, with the greatest part of

the new worker brood removed from cocoons, the colony moved off. No males were seen in this movement; very probably none remained. Three broods: a callow alate male brood; then a huge worker brood; and a further brood of worker larvae.

Colony B-VI (*E. burchelli*) was found on March 31 at 4:30 p. m., bivouacked under some heaped-up branches in the lower part of Lutz Creek. An extensive raid was in progress at the time. When the bivouac cluster was opened a considerable number of alate males (estimated at more than 500 individuals) was found, together with an immense brood of nearly mature worker larvae. In the latter brood numerous indications of spinning activity were observed. When the bivouac-change movement was well under way at 10:00 p. m., alate males were numerous in the procession. Considerably before the termination of the movement a queen (contracted) was observed in the column. In this movement the colony passed to a clustering site high in a large fig tree between Snyder-Molino 2 and Pearson 2, where it entered a statary phase. Thus there was no opportunity to check the departures of the remaining males. On the night of April 20 when the colony again became nomadic, an immense brood of newly emerged callow workers was seen, but no males were observed in the bivouac-change column. Two broods: the remnant of an alate male brood; and an immense brood of workers.

General summary of male production. This evidence from shorter studies of *burchelli* and *hamatum* colonies corroborates the results of the extensive survey of colony B-I in every important respect. The males appear in distinct lots of that sex alone, and at given points in the regular Eciton brood-production cycle, when worker broods might otherwise appear. Thus the male larvae of a given brood exhibit a limited size range at any given time and pass through the respective phases of their development closely in step with one another so that all eventually emerge from their cocoons as callow individuals within a short period of a few days. In other words, a given male brood appears to have essentially the same time relations with the worker brood which preceded it and the one which follows it as would a worker brood under ordinary conditions (cf. Schneirla, 1938, 1944). We have reported three cases (colonies B-I, B-II and H-J) in which male broods were preceded by worker broods, and it may also be noted that in colonies B-I and B-II the male brood was followed by a brood of workers as was the case in colonies B-III, B-IV, B-V, B-VI, H-L and H-M. The conclusion seems inescapable that the eggs of a given male brood must be laid by a single functional queen in each colony, and that this queen delivers a male brood after having produced one or more worker broods. These facts raise some interesting questions for the student of insect genetics.

There is a striking difference between male broods and worker broods, in that while

our single batches of developing workers are all very large with a population of probably more than 20,000 individuals in each, the male broods are all relatively small and number close to 3,000 individuals each. However, rough calculations (based on the relative bulks of preserved material) suggest that we should not be surprised to find the total "tissue bulk" of a male brood at maturity closely approaching or even exceeding that of a worker brood at maturity. The reader should be reminded here that none of the investigated male broods was sampled in the egg or earliest larval collection⁵, so that the number of potential males could be compared with the number of potential workers in respective newly delivered broods.

The chief reason for this hiatus in evidence is readily understood when the complex but regular relationships between brood-production phases and the statary-nomadic changes in colony behavior (Schneirla, 1944) are recalled. The emergence of a new brood are produced when the colony is roughly one-third through a statary phase, at a time when the bivouacs are located in relatively inaccessible places such as hollow trees or logs, all too easily passed by since the raids then generally are small and in the dry season frequently are absent (Schneirla, 1947). Even when a statary bivouac is located, one must go to the heart of the bivouac to sample the eggs or young brood concentrated there, a procedure which for instance was out of the question with the male brood of our record colony B-I in the earliest developmental phase. To obtain such material a concentrated collection procedure will be essential, directed at sampling of brood populations rather than at the gathering of normative behavior data.

Behavior and Behavioral Relationships of Males.

Activities of the male brood considered as a colony energizing factor. When the male larvae are still very small they are packed into boluses in the very center of the bivouac cluster, much as are worker larvae at comparable early stages. This is certainly true of the statary bivouac in which they begin their life, and also of the earliest part of the ensuing nomadic period, except for the time each night when the brood is scattered about in small packets through the bivouac after having been transported on the bivouac-change trail.

There is no reason to believe that with very young the male larval brood is an important factor in raising the general colony excitation threshold to the level of large raids which can pass over at nightfall into bivouac-change process. Thus when colony B-I took to the march on February 28, it presumably a sharp rise in tactuo-chemical stimulation from the immense brood of

⁵ However, an eventual cytological examination of preserved brood samples in very early stages may lead to further male broods to light.

w workers circulating through the community which set off the new behavior developments, rather than stimulation from the small male larvae then packed into a few centrally-located masses. Hypothetically, we may believe that the stimulative role of the male larvae increases rapidly in keeping with their rapid growth rate in the nomadic period (cf. Text-figure 1), so that they take over the principal excitatory function after that of the callow brood has lapsed somewhat.

In this connection it appears significant that the fourth and fifth raids of colony B-I (March 3 and 4) were noticeably smaller than the three first raids of the nomadic period which began on February 28, and that the distance of the nightly bivouac-change movements was considerably reduced as compared with the preceding ones. The movement of March 2 carried over only 30 meters, that of March 3 over 19 meters, and on the night of March 4 the colony shifted its bivouac only 8 meters, as compared with movements of 110 and 75 meters in the first two nights respectively. It is probable that the noticeable decline in the vigor of raids and in the extent of nomadic movements at this time was based upon a reduction of effective stimulation from the broods. We have suggested previously (Schneirla, 1944) that the stimulative effect exerted by new callows drops off sharply within the few days after their emergence. At that time a very young larval male brood (relatively small as it is in numbers) may be still rather weak in energizing the colony, although both of these brood factors may act together in keeping the colony above the statary level of activity.

For the remainder of the nomadic period during which the B-I male larvae were growing rapidly, the daily raids were large and all of the nightly bivouac-change movements were relatively lengthy affairs carrying over more than 100 meters of ground. Then, as we have seen, the colony became statary on the day when most of the mature larvae had become enclosed. It remained statary with small daily raids or no raids on given days, until identifiable reflex activities of the enclosed but nearly mature male pupae occurred. Then the daily raids became increasingly extensive and vigorous, and the colony became nomadic at the time when the major part of the male brood had emerged as callows.

This is the same type of coincidence of brood condition and colony behavior which we have identified when worker broods are present in *Eciton* colonies. It indicates that male broods have much the same trophalactic (i. e., social-stimulative) relationship and colony-energizing function as have worker broods. A consideration of the general behavior evidence concerning males further supports this view.

Responses of workers to the male larvae. When they are very young, the male larvae are gathered together into a few packets generally kept near the center of the bivouac.

These boluses of larvae thereby are somewhat isolated from the workers of the general colony, although they are the scene of much activity on the part of the diminutive workers minor. The minima not only crowd upon the external surface of the massed larvae, but also push into the interior through narrow galleries among the larvae. Presumably, as with young worker broods, the workers minor are more or less consistently occupied with licking the tiny larvae of the young brood and palpating them with antennae. Presumably also, at some time before the colony leaves its statary bivouac (e. g., before February 28 in colony B-I), larval feeding also begins. Although direct evidence upon these early events is very scanty at the present time as far as male broods are concerned, the state of affairs probably is similar to that previously observed with young larval worker broods.

We have some direct observational evidence for the colony relations of male larval broods after the colony takes to the march, when there is a much more rapid increase in body size than with worker larvae and a proportionately rapid increase in the scope and vigor of larval activities. The almost incessant twisting and squirming movements of the larvae, which are increased noticeably as workers touch them antennally or run across them, act in turn to increase the activities of the workers. The result is that, as these stimulative relationships increase to the point of involving workers through the intermediate types, the workers frequently pick up the larvae and hold them individually, or carry them about. As the brood advances in development, it is thereby more widely distributed through the bivouac cluster. This change obviously increases the stimulative scope of the brood, and as with worker broods, that development is related causally to wide increases in the extra-bivouac activities of the colony (cf. Schneirla, 1938).

Thus it seems that a male larval brood enters into trophalactic relations with the adult membership of the colony which serve to increase colony "drive" much as does the stimulative effect of a worker brood. The fact that the population of a male brood in species of *Eciton* (*Eciton*) contains only about one-tenth as many individuals as do worker broods is not contradictory on this score. To resolve the difficulty it is only necessary to consider that, at comparable growth stages, the body size of any male larva in the nearly homogeneous brood is many times that of the median size larvae in a worker brood. Accordingly, we should expect that the stimulative effect of each male larva (both in tactual effects through movements and chemostimulative effects through cuticular secretions) would be much greater than that exerted by worker larvae with their much smaller size, strength, and body area. From our observations, such is undoubtedly the case. For instance, while in the bivouac even the largest worker larva generally is

held by no more than one or two workers, it is not uncommon to see a bulky male larva held in place by a dozen or more workers. Based upon such differences, interesting variations appear in certain extra-bivouac activities when a male brood in a fairly advanced larval stage is present.

Behavior involved in the nomadic transfer of a larval male brood. The transportation of a young larval worker brood by a nomadic colony occasions no particular difficulties, since the tiny larvae are carried in small packets by individual workers, and in the night-time hours following the movements are gathered together into the center of the new bivouac. When the worker larvae are larger and even when they are nearing maturity and are close to maximal size, they are carried readily by individual workers, each larva slung beneath the body of a carrier, the anterior segments of the larva gripped in the mandibles of the carrier. Little difficulty is involved except in starting out from the old bivouac, when a single larva often is gripped by numerous workers pulling against one another. This often happens when a worker has grasped a larva much too large for it to carry in straight-forward progress, and a circuitous tugging results which attracts other workers to the scene. Usually as a result of these tussles one of the larger intermediate workers large enough to deal with the burden finally keeps possession of the larva, and notwithstanding her load moves unobstructed ahead as a member of the column. Even in the absence of quantitative data it is safe to say that in the Eciton bivouac-change column there exists a direct relationship between bulk of burden and size of the worker carrying it.⁶

Difficulties due to excessively bulky burdens do not occur in the first few nomadic movements of a colony with an early brood of male larvae. In fact, despite a vigilant observation of the first three bivouac-changes of colony B-I when its male larval brood was small, the brood escaped my notice and was first sampled from the bivouac on the fourth day. The observation of an increasingly striking set of events in the eighth and ninth movements of the period on the nights of March 7 and 8 first brought out some notable differences between the transportation of larval worker and of larval male broods.

In the early stages of the bivouac-change movement lugging of the bulky male larvae from the bivouac begins when each larva becomes the center of much worker activity. A very circuitous, hit and miss process then is involved in getting a larva into carriage on the trail. At first the unwieldy object is pulled around haphazardly in different directions near the bivouac by numerous workers tugging at it, so that it is yanked and

dragged on and off the trail repeatedly. There is much bumping and colliding of bodies moving variously at "cross purposes," in a hectic time-consuming process. In the course of this largely random activity, more and more workers come to mill about with increasing numbers of larvae at the trail-base close to the bivouac. Added to the difficulty of somehow attaining a coordination of worker activities in carrying individual larvae, many special interferences are presented by an irregular terrain complicated by leaves, brush and tangled vines. But gradually, in the course of two or more hours as the bivouac-change movement gets under way, a development arises from the tussle and struggle which in the end helps to resolve the whole difficulty very nicely.

In the yanking and pulling about of larvae by groups of workers, by degrees more and more of the workers drop out of the activity and huddle or stretch out motionless on the spot where a summation of swarming-under or rough treatment occurs. By small steps and very slowly a layer of clustered ants thereby forms over the trail itself and at the sides of the trail near the bivouac. Over this "ant roadway" other workers run and pull larvae about, incidentally smoothing the substratum further by forcing protruding parts of the cluster to shift position. Of course the roadway is not of uniform thickness, since the ants cluster most readily at the edges of leaf obstacles and at terrain depressions and similar points of obstruction where the greatest amount of pellmell struggle and bumping about of bodies is certain to occur.

The early stages of this complicated process must be observed in detail and in sequence, if one is to appreciate just what causes workers to form the "roadway." Watching individual workers in the push, we note that the elements of the roadway are recruited from among those individuals that are repeatedly buffeted and overrun within limited intervals of time. Once they are out of general activity, such workers lie motionless except for a vibration of antennae, stretched in place by catching with their tarsal hooks into objects such as leaf edges or the projecting body parts (generally legs) of other workers. Workers may thus lie in place immobilized for hours as the procession rushes over them. Evidently a repetition of tactual stimulation is essential to keep the workers immobilized in the pavement of bodies. For as the column gets under way and side eddies of traffic cease to pass over ants clustered at places away from the main line or in remote depressions where larvae happened to roll in the early struggle, workers in such isolated clusters presently begin to stir, disengage themselves, and run off.

The roadway of clustered workers is widest close to the bivouac and progressively narrower in trail sections farther out. An even more striking reminder that the roadway arises indirectly out of difficulties in

⁶ Lutz (1929) reported essentially the same conclusion for the carrying of leaf-segments by workers of *Atta cephalotes*. The average load under the conditions of Lutz's survey was roughly five milligrams more than twice the weight of the carrier.

transporting bulky objects over rough ground, is the fact that it is started at the old bivouac site and laid down progressively over the trail toward the new site. In the innermost stretches of trail (e. g., more than 5-100 meters from the old bivouac) the band is thin and narrow or even absent, except where irregularities and obstructions in the route such as upturned leaves have produced serious interferences with the transportation of larvae. When a male larval brood reaches maturity and occasions the greatest difficulties in transportation, the roadway is most likely to be clearly formed as a meandering ribbon of clustered workers extending perhaps the entire distance from old to new bivouac sites. The adaptive significance of the roadway, as a relatively even surface over which the huge male larvae can be moved to the new clustering site, does not require much emphasis here.

The indirect manner in which the ant roadway comes about is further revealed by observations upon changes in the carrying of larvae. In some respects the changes are similar to those involved in the transportation of worker larvae as first described above. The building of the roadway is the result of hours of laborious changes during which a directionalized column arises. To indicate how the shift from inefficiency to efficiency occurs in larva-carrying, for the sake of clarity it is best to choose a time after the shift from the old bivouac is fairly well under way. Then each male larva is dragged from the bivouac by several workers of nearly all sizes except majors, clutching and tugging at it on all sides. In the course of much thrashing about with the burden most of these are shuffled off and rolled underfoot, to furnish a source of recruits for the roadway. Finally, as a rule only two of the larger intermediate workers retain their holds and carry the larva in the direction of general movement. Characteristically they run in tandem with the larva slung beneath their bodies, straddling it with their legs, one clutching the burden in her mandibles at the anterior segments while the other catches hold behind the midsection. Relatively immature male larvae may be transported in other ways as well, and in carrying these the smaller workers may participate all of the way; however, with bulky, advanced larvae there is least variation in the size of burden-bearers since smaller workers are largely eliminated during the initial tussle. Although both early and late in the movement difficulties such as those described occur at the start of the journey, once the eventual carriers are under way with their burden on a fairly well-formed "roadway," they make surprisingly good headway and there is a minimum of stoppage. The occurrence of the roadway, typical of bivouac-change movements when advanced male larvae (but generally not worker larvae) are transported, is an expression of the high stimulative effect which the maturing and bulky males, individually and collectively,

exert upon the worker membership of the colony.

Behavior associated with enclosure and pupation of the male brood. Colonies of *E. burchelli* and *E. hamatum* cease nomadic movements when their male larval broods mature and become enclosed, and remain stationary until the colony's male brood has completed its pupation. In these respects the results for case B-I coincide with data from numerous other colonies of both species.

The spinning of cocoons by male larvae resembles in general outline the process as described by Beebe (1919) and by Schneirla (1934) for Eciton worker broods. The difference is that all phases of the process occur in a much more striking way when male larvae are involved. Some of the highlights from the B-I record will stand as representative.

The last nomadic nest of colony B-I, when its male brood was at maturity, was established in a shallow mammal burrow. Larval spinning must have occurred during this day (3/9/46) since many of the larvae picked out from the bivouac-change column of the same night were provided with thin envelopes. Later that night scattered instances of spinning were observed on the interior floor of the large hollow tree into which the colony passed. However, the bivouac cluster was formed within the cavity of the tree just above the wide opening at its base, and most of the spinning evidently occurred in the upper spaces. Much of the time during the first three stationary days (March 10-12) the cavity walls and the ground both within and immediately around the tree were covered with throngs of milling ants. Both day and night, occasional concentrations of workers were observed around larvae which had been lugged to the floor of the cavity where spinning took place on a carpet of wood dust. Evidently the enclosure of only a minor part of the male brood was begun in this way, judging by the number of similar groups observed by flash-light in activity around the bivouac, and by a constant downward drifting of fine wood detritus through the air. This fall continued for about five days, until there had accumulated on the broad floor of the cavity a wide conical heap of finely divided woody material more than 15 cm. deep in one or two places.

Some notes on events in colony B-I typify the details of behavior. "On the floor of the tree hollow (6:15 p. m., March 12) here and there are groups of a dozen or more workers gathered around one of the large larvae, touching it at intervals with antennae and mouth parts as its anterior end twists about in spinning, and tugging at it intermittently. Each larva is the center of much commotion, particularly when the joint tugging of numerous workers shifts or rolls it about on the gently sloping sides of the wood-dust mound. Other similar groups can be seen stationed at intervals on the nearly vertical back interior wall of the tree, with a variable number of workers holding fast to each larva

engaged in spinning. This number often grows into a sizable mass of squirming bodies around a larva which (through its own movements or because of a flurry among the ants) happens to slip momentarily from the mandibles of workers which have been holding it in place."

None of the larvae thus engaged in spinning outside the bivouac were enclosed by more than thin transparent envelopes, whereas after March 11 the bivouac contained a rapidly growing number of larvae with heavier and translucent brownish cases. The inference is that the early stages of enclosure take place outside the bivouac, whereas once the envelope is started it may be completed while the larva is held within the mass of ants in the bivouac cluster itself. The ants seem to drag out only naked larvae or larvae in the early stages of spinning.

When spinning is completed, colony activity decreases markedly. For example, on March 14 practically all of the B-1 brood was enclosed in brown cases, and no spinning was observed outside the bivouac. At 8:30 a. m. a few hundred ants were running about over the floor of the cavity, and there were two or three columns which extended only a meter or two outside the tree. No raiding system was formed on this day; only a limited raiding system formed on March 15, and there was none on March 16. Judged in terms of amount of activity outside the bivouac, particularly the frequency and the size of raids, the general activity of the colony fell to a low point after the larval brood was enclosed. It is significant that although daily raids occurred during the first four days of the statary period, in which brood-enclosure evidently was completed, no raids developed and colony activity was minimal on the three following days. Activity in B-1 remained at a relatively low ebb, with no raids occurring on half of the days, through the central part of the statary period until March 26. This was the quiescent period of pupation in the male brood.

Thereafter raids occurred daily, increasing in vigor, until on March 30 a recognizable nomadic condition arose. The increase in colony activity appeared coincidentally with certain new brood developments. On March 27 there were reflex movements of antennae and tarsi, as well as general trunk contractions in some of the pupae, readily perceptible to the naked eye. A few empty male pupa cases were found below the bivouac on that day. The number was considerably greater on March 29, when cocoon-opening by workers was found. This process is similar to that previously described for the delivery of a worker brood (Schneirla, 1934, 1938). The difference is that each male cocoon is the center of a far greater commotion as it is held by struggling workers stationed in the bivouac structure.

As is the case with worker broods, the colony begins its nomadic movements when the major part of the mature pupal brood has emerged. Also, as with worker broods,

a critical species difference appears in that in the first movement of *burchelli* colonies a considerable part of the brood (nearly one-third in given instances) may be carried along in column in unopened cases, whereas in *hamatum* colonies the unemerged increment is much smaller or even absent. Hence in the first *burchelli* movements one may observe numbers of bulky male cocoons carried along in a bivouac-change column which is thronged by newly emerged callow males.

Behavior of callow males and colony responses to them. We have set forth the principal facts with respect to the behavior relations of callow males to the colony, in records condensed in an earlier section of this paper. Within the period of about three weeks required for the complete discharge of a male brood from its parent colony, only after dusk do the callow males appear outside the bivouac. In the daytime the males hang in the cluster, among the workers, but in the hours after nightfall they may be seen in small numbers as a rule running about close to the bivouac. Each of them is attended by a small group of workers which follow him closely as he runs about circuitously and erratically, a few of them clinging to his wings and gaster, others riding upon him. From time to time a relatively free male may take short hopping runs, flit his wings nervously and even leave the ground in short flights, frequently after having mounted a stalk or vine. At intervals, as the night advances, the males take off in flight from low vegetation. Although one gets the impression that the worker "hangers-on" impede the flight-escape of males, it is possible that males sometimes fly off carrying workers with them. A few such escapes were observed in the present study.

As a rule, not many of the callow males leave the bivouac until the workers have begun their regular exodus in the bivouac-change movement. Then the alates take their exit from the cluster among the workers, each of them followed rather closely in the procession by a group of workers. Clumsy behavior in beginning the movement is typical of males, with frequent stops and returns occurring before they get under way in the column from the bivouac. During traffic interruptions which are occasioned by such behavior, males with their worker retinues may separate from the column and enter the zone around the bivouac where males are skipping and flitting about more or less independently.

Once they are under way in the regular bivouac-change columns, the alate males move along under their own power, at a regular pace and with closed wings. One gets the impression, from watching the movements of a given colony evening after evening, that the trail-running of males undergoes an improvement in the course of time in that after a few nights progress seems to be more regular than at first and there are fewer returns and interruptions. The

males often run in single file with workers; often males run together in file. The clinging and crowding workers generally retard the pace of the alates somewhat, and the paths are blocked variously (by the slowness of other males in particular), so that colonies with alate male broods sometimes require the entire night and perhaps the early daylight hours as well to complete their movements.

When the new bivouac cluster is reached, most of the alates stream directly into it with the workers. It is the first males to reach the new site, before the cluster has been well started, that may get away from the main group of workers and run about in the vicinity. Some take-off flights may result.

Events after departure from colony of origin. Our findings show that after a brood of perhaps 3,000 winged males has emerged, these alates leave the parent colony by flying. However, in the colonies for which emergence of callow alates was observed, no escapes were recorded on the first three or four nights after the cases were removed. Then, a given number of males takes off nightly by flying away in the course of excitatory activity in the vicinity of the bivouac, until in the course of about three weeks after emergence most or all of the winged males have left the bivouac of origin.

Direct observations show that *Eciton* males are capable of strong maintained flight once they are under way, so that with the assistance of air currents some of them must get several hundred meters if not greater distances from the parent colony. From early February of 1946 at Barro Colorado the winged males of various *Eciton* (*Labidus*) and *E. (Neivamyrmex)* species were taken nearly every night at the laboratory lights and often on the white reflecting board at the laboratory clearing, as well as in the small light trap set at various places within the forest. The alates of these groups also were taken occasionally by hand when attracted at night to the reflector of the 5-cell headlamp which I used in the forest. However, our study concerns male-production in the species of *Eciton* (*Eciton*) particularly, and for some reason the alates of species in this subgenus were almost never taken at lights in these ways. The exceptions occurred when I worked with a light within the area around a colony from which alates were known to be issuing at the time.

Special field and laboratory tests show that the males are able to follow the chemical trails of their own colony or another colony of their species. Alate males ordinarily do not leave the bivouac of their colony in the daytime. On the other hand dealate males

TABLE II.

Dealate males of *Eciton* (*Eciton*) species found on Barro Colorado I. during the period February—June of 1946.

Date of capture	Colony and species	Time of day	Locality and general circumstances	Alates present in the colony	No. taken
March 3	B-I <i>E. burchelli</i>	8:00 p.m.	Running in bivouac-change column with workers, en route toward new bivouac	None; only males in early larval stage	7
March 4	B-I <i>E. burchelli</i>	9:00 p.m.	Running with workers in bivouac-change column	None; only males in early larval stage	3
March 8	B-IV <i>E. burchelli</i>	7:40 p.m.	Approaching old bivouac in column of workers	Remnants of alate brood present	1
March 11	B-IV <i>E. burchelli</i>	9:00 p.m.	Approaching new bivouac in column of workers during bivouac-change	Remnants of alate brood present	1
March 27	H-B <i>E. hamatum</i>	10:45 a.m.	Moving with workers in column a few cm. from the bivouac	No male brood produced by H-B	1
April 6	B-I <i>E. burchelli</i>	8:40 p.m.	Running toward the old bivouac in column of workers	Own alates present in bivouac	1
April 9	H-L <i>E. hamatum</i>	10:00 a.m.	Captured from central part of colony bivouac cluster	Newly emerged alates present	1
April 12	H-H <i>E. hamatum</i>	10:15 a.m.	Captured from central part of colony bivouac cluster	No male brood produced by H-H	2
May 5	B-I <i>E. burchelli</i>	10:30 p.m.	Taken from bivouac-change column en route toward new bivouac	Few if any alates remain from own male brood	1
May 13	H-B <i>E. hamatum</i>	7:45 p.m.	Standing among workers on log close to bivouac, among larvae (cocoon-spinning)	No male brood produced by H-B	1

have been taken on occasion in the present study and by others (Wheeler, 1912; Reichensperger, 1926), running about on the raiding trails of their species in the daytime. Appropriate tests show that after their flight males are accepted into groups of workers of their own or other colonies of their species. It is probable that the chief means of getting into some colony after the flight is through the following of a chemical trail which is crossed accidentally as the scattered males run about over the forest floor.

Although we have little direct evidence on what happens to alate males once they leave the parent colony on their flights, from certain facts the general nature of events may be suggested. In the first place, laboratory tests indicate that a considerable amount of flying leads to loss of the wings within a few hours, hence our attention turns to occurrences involving dealate males.

Table II shows that dealate males were discovered in association with Eciton colonies on ten different occasions in this study. In five of these instances (B-I, March 3; B-I, March 4; H-B, March 27; H-H, April 12; and H-B, May 13), the dealates clearly must have originated in another colony of the species. For example, a limited number of dealates was found in the bivouac-change columns of colony B-I on two successive evenings at a time considerably before the male brood of this colony had even completed the larval stage, but at a time when a *burckhelli* colony with alate males was known to be located in bivouac relatively close by. On the night of March 3 seven dealate *burckhelli* males were captured while running at intervals of a few meters apart in the B-I column. Obviously these males must have come from some other *burckhelli* colony, since at the time the male brood of colony B-I was in its early larval stage. The most likely source was another *burckhelli* colony with a large brood of escaping alate males which at the time was bivouacked only about 350 meters from the location of colony B-I. On the following night, when the colonies were still no more than 450 meters apart, three additional dealate males were found in the B-I column. Subsequently these colonies moved divergently, and no further dealates were observed in colony B-I until May 5. The capture of dealate males from two different *hamatum* colonies (H-B, on March 27 and May 13; H-H, on April 12) took place when no alates were present and only worker broods had been produced. In four of the cases (B-IV, March 8; B-IV, March 11; B-I, April 6; and H-L, April 9) the dealate individuals were found at times when alate males produced by the same colony were also present, and may have been returned males of the same brood. The case of colony B-I on May 5 is more doubtful. Although a few survivors of the alate male brood may have been present at the time, none had been seen during the preceding week. Our cases divide nearly equally into those in which the dealate males must have come from another colony of the spe-

cies, and those in which they may have originated in the colony in which they were taken. Although, in some instances males evidently return to their own colonies after the flight, the surprising thing is that so few dealates were found in colonies known to contain alates. Evidently post-flight returns into the colony of origin are exceptional.⁷

As Table II shows, dealate males were taken in this study both in bivouac-change columns at night and in raiding columns in the daytime (and under the latter condition also by Wheeler, 1912, and by Reichensperger, 1926). There is no evidence that dealate males leave the bivouac of the host colony in the daytime to run the raiding trails, and it seems more probable that instances of dealates on raiding trails involve newly dealated individuals that have encountered the chemical routes of a colony after alighting but have not yet entered its bivouac. Some of our night-time captures of dealates on bivouac-change trails may similarly involve newly alighted individuals; however, it is also very likely that in others of these instances the males were running in the movement after having spent one or more days in the host colony. The case of the males found in the B-I column on the nights of March 3 and 4, as the circumstances described above suggest, seems the clearest instance of probable night entrance into a column. Other facts suggest that such entrances may occur either by night or by day, when stray males chance upon and follow trails.

As mentioned above, our laboratory and field tests show that males of *E. burckhelli* and *E. hamatum* are capable of following the chemical trails of their own colony or another colony of their species. For instance, on numerous occasions dealate males were placed close to a circular column formed in the laboratory by workers of a strange colony of their species. In virtually all cases the male finally entered the column more or less readily after chancing upon the trail, and soon was running on the endless route among the workers, although typically with a clumsiness that contrasted notably with the typical stereotyped precision of the ordinary workers. For their part the workers generally accept any stray dealates one may present from other colonies, on occasion nipping at the newcomer for a time, but generally indicating in their behavior that he exercises a considerable chemo-receptive attractive effect upon them. When the new male is set down experimentally at a raiding trail in the field, as a rule he is taken into column by the workers. Typically they are soon clustered around him and, when he eventually moves off on the trail, he has an entourage of closely following workers some of whom cling to his body or even ride upon him. The attractive effect of Eciton males upon work-

⁷ The latter type of case very probably appears with misrepresentative frequency in our records, since colonies with male broods were examined more frequently in detail than were others.

ers resembles that of the queen (Schneirla, 1944), with the difference that the latter appears to be definitely more powerful.

SUMMARY AND DISCUSSION.

It is clear that in the area of this study and for the *Eciton* species investigated, the production of males is limited to the dry season. In studies on Barro Colorado Island (confined to the rainy season (Schneirla, 1933, 1938, 1944) only worker forms have been found in *Eciton* broods, but in the dry season of 1946 male broods at all stages were discovered in colonies of the same species (*E. hamatum* and *E. burchelli*). Moreover, there appears to be a species difference in susceptibility to whatever conditions account for male-production. In our records for the 1946 dry season male broods appeared roughly one month earlier in colonies of *E. burchelli* than in colonies of *E. hamatum*.⁸ This difference may be added provisionally to other differences previously described in the raiding, bivouacking and general behavior of these two species of subgenus *Eciton* (*Eciton*).

The discovery of immature male *Eciton* broods has been reported in three instances from other localities. The first of these is not strictly comparable to our results, since it concerned a species of the hypogaecic subgenus *Neivamyrmex* (= *Acamatus*). The engineer Hubrich sent to Carlos Bruch (1924) specimens of advanced male pupae of *E. (Neiv.) hetschkoi* taken at the end of July (in "winter") 1924 in the Sierra Alta Gracia of northern Argentina. Numerous enclosed male pupae approximately 13 mm. in length were found in the bivouac cluster, which was beneath a large tree trunk. This finding, together with various discoveries of mature male broods to be noted below, suggests that in *Neivamyrmex* species also the males appear in distinctive broods of their own sex alone.

The first discovery of a developing male brood in any species of *Eciton* (*Eciton*) was reported by Wheeler (1921). The find was made at the Kartabo station in British Guiana on July 17, 1920, at the end of a short semiannual wet period. A colony of *E. burchelli* which Drs. Wheeler and Emerson drove with smoke from its bivouac in a hollow tree was found to have a brood of a few hundred mature male pupae in cocoons. A brood of male pupae somewhat less advanced than in the above instance was found by Schneirla (1947) during early April of 1945 in a colony of *E. hamatum* in the area of the upper Coatzacoalcas R. in southern Mexico. The conditions in this case were similar to those of our 1946 Panama records given in the present paper, in that a brood of more than 1,000 pupae was found during the latter half of a well-marked annual dry season,

in a colony which was definitely "statory" at the time. A further resemblance is found in the fact that in the Kartabo and S. Mexico cases a large brood of very young (evidently worker) larvae was present in addition to the male pupal brood, a relationship of broods which holds uniformly in our 1946 Panama records.

The present study involved the investigation of particular colonies of *E. hamatum* and *E. burchelli* over considerable intervals of time while male broods were undergoing their development. The results from the respective instances, which represent all stages of male development, indicate that a given male brood appears at a predictable time in the colony brood-production process, that is, occurs in a definite temporal relation to preceding and following (worker) broods. Thus the present results for male broods fit the timing of the *Eciton* reproductive process as previously described for the rainy season (Schneirla, 1944). Our results indicate the prevalence of a pattern of events which is adequately represented by the case of *E. burchelli* colony B-I. Numerous other evidence given above supports this fully investigated case in showing that the eggs of a male brood must be laid (in both our test species) in the first part of a statory period when an enclosed brood of worker forms entering pupation is present, and that when this male brood enters its pre-pupal phase during the next statory period of the colony, a huge new brood of (worker) eggs is then laid by the queen.

The expression "*the queen*" is used advisedly here, since from our results it is evident that the eggs of an all-male brood must be laid by the single functional dichthadiigyne responsible for the delivery of the large worker broods which precede and follow the males in a given colony. Our results invariably indicate a high degree of regularity in the time relationships of male and worker broods found in particular colonies, without any evidence that more than one functional queen is present in a given case.⁹

There is one report in the literature which suggests that conditions in other *Eciton* subgenera may be similar to those evidently prevalent in species of *Eciton* (*Eciton*). That is the discovery of a large colony of *E. (Lab.) praedator* by Luederwaldt (1918) on October 23, 1916, bivouacked in an old termite nest in a garden at São Paulo, Brazil. This colony possessed a brood of enclosed worker pupae, as well as numerous empty cocoons about 20 mm. in length from which males were thought to have emerged. Furthermore, the queen was physogastric at the time and masses of newly laid eggs were found—a set of circumstances suggesting a regular succession of broods, with one of them evidently a male brood.

⁸ It is well known that seasonal production of males as well as females is common among the other subfamilies of ants. Characteristic differences in the time of year at which fertile forms are produced have been described by Talbot (1945) for four temperate-zone species representing two ant subfamilies.

⁹ In a subsequent paper the conditions under which a second queen was found in colony B-I will be reported. Various reliable circumstances made it clear that she was not the functional queen of this colony but a new supernumerary dichthadiigyne.

Our findings on the male broods in species of *Eciton* (*Eciton*) indicate that such broods contain only male individuals. They also suggest that very possibly no colony has more than one such brood in a given season and that otherwise worker broods are produced.¹⁰ It is also quite probable that some of the colonies produce no males whatever. At any rate we have the record of colony H-B (*E. hamatum*) which produced four large worker broods but no male broods during the 1946 dry season. In this survey more than fifty colonies of *Eciton* (*Eciton*) species were studied for intervals of a few days or for longer intervals, yet indications of male-production were found in but eleven of these cases. Although the possible errors of sampling were much greater when *Ecitons* were searched for in five different localities of southern Mexico in the dry season of 1945 (Schneirla, 1947), it is worth repeating here that only one of more than 20 *Eciton* (*Eciton*) colonies then studied had a male brood at the time. The Panama results suggest that very few if any colonies of this subgenus have more than one male brood per season.

From our evidence the influence of a male brood upon colony behavior is very similar to that which we have described for worker broods (Schneirla, 1944). As with worker broods, the energizing or "drive" function of a male brood is introduced and is removed in an essentially all-or-none fashion, in dependence upon the growth stage reached by the brood. Clearly the basis of this factor is the capacity of the queen to complete laying the eggs of a given male brood within a few days, so that the entire brood passes through the successive stages of development in step. Consequently, at any given time all individuals in the male brood exert similar effects upon the general colony.

We have found that when male broods appear in *Eciton* (*Eciton*) colonies there are no important interruptions or differences in the nomadic-statory cycle of colony behavior, which occurs substantially as when worker broods are present. Colonies with fairly advanced broods of male larvae are found in the nomadic condition, staging large daily raids that terminate each night in a bivouac-change movement of the entire colony. As with worker broods, the colony shifts from nomadic to statory behavior precisely at the time when its male brood has completed larval development and is spinning cocoons. Then later, when the enclosed male brood has completed its pupation, a further nomadic period begins with the emergence of the callow males from their cocoons.

The occurrence of male broods evidently does not disturb the timing of nomadic-statory phases in any important way, since we have found no identifiable differences in the duration of the phases and in the total developmental time of male and of worker broods. We have inferred that the inclusive

developmental period of a male brood requires about 45 days, and have found in the case of three *burchelli* colonies that the male spend close to 21 days of this time enclosed in cocoons, just as do worker broods. From the routine facts alone, as concerns the intensity of daily raids and the occurrence or non-occurrence of night-time movements it would be difficult to tell which type of brood, male or worker, was present.

As we have suggested above, the basis of the concomitant changes in male brood and colony behavior is found, as with worker broods, in the trophallactic relationships of workers and brood (Wheeler, 1928; Schneirla, 1941). Our field observations and specific laboratory studies show that male larvae stimulate the workers both tactually and chemically, and thereby exert a distinctive energizing effect upon the workers. We have found "nomadic" colonies somewhat sluggish when their male larvae are still small, and have interpreted this condition as an insufficiency of the energizing effect of a male larval brood to maintain colony activity at its peak early in the nomadic period, at the time when the stimulative effect of a callow worker brood (which initiated the period) has waned. The stimulative effect of the male larvae soon increases greatly in keeping with a rapid advance in their size and activities, a change which evidently provides the essential basis for a marked rise in general colony activity. In the daytime the large larvae are spread well throughout the bivouac, each held by a group of workers as the center of a rather extensive zone of stimulation in the cluster. And at night in the colony movement, the bustle and complexity of events in the transportation of the bulky larvae emphasize the great stimulative effect which the brood exerts upon the colony. One outstanding event that is peculiar to the relations of the male brood to worker behavior is the formation of the "ant roadway." We find that although a male brood is roughly only one-tenth as numerous as a typical worker brood, after early development its total stimulative effect appears to equal or even exceed that of a worker brood at corresponding stages.

There is no support in *Eciton* behavior for the assumption of Brauns (1901) and others that doryline colonies must remain in place while breeding the sexual forms because it is impossible to transport the large larvae of these forms. We have ample evidence that *Eciton* colonies are able to carry along the male larvae nightly in bivouac-change movements so long as these larvae are immature and unenclosed, even when the larvae are maximal in size and very unhandy to lug along in column. The eventual stoppage of colony movements when the male larval brood is mature depends upon quite different causes than mere bulkiness of the brood.

The manner in which *Eciton* colonies drop to minimal activity once their male brood are enclosed contrasts strongly with the

¹⁰ The circumstances of queen-production are unknown at the present time.

rescendo which occurs in colony activity as the maturing pupae begin their reflex stirring within cocoons. These activities arouse the workers to a mounting pitch of activity within and outside the bivouac, which eventuates in the shucking of callow males from their cases and the transition of the colony into a new nomadic phase. It is during this period of about two weeks that most of the few thousand males leave the colony. This concurrence of events has a particular adaptive value, as we shall see.

The exodus of winged doryline males from their nests has been reported in numerous instances in the literature. For Old World dorylines, Brauns (1901) reported the notes of G. A. Marshall on a colony of *Dorylus* observed in Rhodesia (Africa). In this case, large numbers of alate males emerged from the extensive subterranean excavations of the colony, with the workers evidently driving out the males or even pulling them from the nest. In India, Wroughton (1892) saw the workers of *Aenictus wroughtoni* on two successive days apparently driving winged males from the nest of the colony beneath a verandah floor. Santschi (1908) discovered beneath a dye-shop oven in Tunis a large *Typhlopone fulvus* nest from which hundreds of males took flight in the late afternoon on six consecutive days.

The previous Eciton observations are relatively few, and are limited to the hypogaecic species. A number of winged males was found by Hetschko (Mayr, 1886) in the subterranean galleries of an *E. (Acam.) hetschkoi* nest excavated by him at Paraná, Brazil. Wheeler (1900) reported witnessing the exit of males in numbers from a nest of *E. (Acam.) schmitti* in dry soil, near Austin, Texas. In the Sierra de la Ventana of Argentina on February 16, 1916, Bruch (1916) saw numerous male individuals erupting one evening from a nest of *E. (Acam.) strobili* under the foundation of a building. In a colony of *E. (Acam.) spegazzinii* found in a comparable situation at Bella Vista, Argentina, by Gallardo (1915) in April, 1914, eight days after a group of about 50 winged males had been dug out from one part of the nest the workers opened a second exit between stones, from which numerous males presently emerged and flew off. Workers of this species were observed in the same locality in February of 1917, 1918 and 1919, but appeared to be without males; however, in December of 1916 an exodus of males was observed from an *E. (Acam.) spegazzinii* nest in another section of Buenos Aires province (Gallardo, 1920).

These observations support the conclusion that males of the hypogaecic subgenus *Acamatus* (= *Neivamyrmex*) develop in specific broods which emerge from their cocoons within limited periods of time, as do those of *Eciton (Eciton)* species. Smith (1927) concluded, that since alate *Neivamyrmex* males were taken by Wheeler in Texas during October of different years, and since he himself received specimens from the mid-

dle South captured in mid-November, "the males do not reach maturity until late in the season." We may suspect that the males of these species characteristically develop seasonally and leave the parent colony in considerable numbers at given times.

Doryline males of certain species are readily taken at lights in the tropics at given times of year. Vosseler (1905) reported the impression that the males of African species swarm to lights in numbers at times when major changes in humidity occur. Wheeler and Long (1901) reported that the males of *E. (Acam.) schmitti* fly to lights during the spring and early summer in Texas; later Wheeler (1913) noted that males of *E. (Lab.) coecum* are common about lights in the Austin area from early March to late in April. Males of *E. (Acam.) carolinense* were taken by W. Davis in Georgia in June, 1908 (Wheeler, 1921). Von Ihering (1912), who kept a colony of *E. (Lab.) coecum* under observation for about four months while it occupied the same site, stated that in Brazil flights of *Eciton* males generally come in midsummer, particularly in the months of December to February. Also, he noted that the annual flights varied; for example, whereas large numbers of males representing at least six species were taken at lights in the year 1910-1911, the results were sparse the following year. As noted by Gallardo (1920), the males of *E. (Acam.) strobili* are frequently seen in the Argentine around house lights during the spring and summer, where Strobel (Mayr, 1886) took them in numbers during the summer months of December to February. Sumichrast (1868) reported capturing numerous *Eciton* males at lights during the first rains, in the Cordoba area of Vera Cruz in Mexico. At the lights of the Kartabo Laboratory in British Guiana, Wheeler (1921) took a few males of different *Eciton* species each night between July 26 and August 31, 1920. Of 41 alate male specimens, two were identified as *E. burckhelli* males, and 39 were attributed to a colony of *Cheliomyrmex nortoni* nesting close behind the laboratory building.

It will be noted that with the exception of Wheeler's capture of two *E. burckhelli* males in British Guiana, all of these reports concern *Labidus* and *Acamatus* species. The difference cannot be attributed to chance, for at Barro Colorado Island during the spring months of 1946 males of the hypogaecic species were commonly taken at the lights of the laboratory, a few dozen meters from the forest edge, and at light traps within the forest itself, whereas no males of the *Eciton (Eciton)* species were taken at the laboratory and few were taken at forest light traps. The difference may be due in part to typical habitat differences among the subgenera, perhaps to unknown differences in flight (e. g., range) and responses (e. g., to light) of the males.

The present study has furnished some direct evidence concerning the manner in which alate *Eciton* males are dispersed from

their parent colonies. The alates ordinarily remain within the bivouac during the day, emerging only after nightfall. One important factor as laboratory tests show is their withdrawal from very bright light. The males of *Eciton* (*Eciton*) species have large compound eyes as well as dorsal ocelli, and reactions to light may play more than one rôle in their behavior.

The departure flights of males, once they begin, always occur after nightfall. However, very few flights are to be observed within the first nights after a given brood has emerged. Possibly after emergence there are certain maturational processes which must run their course before the flight can occur, comparable to those reported by Snodgrass (1925) for the drone honeybee. In addition there are certain extrinsic circumstances which appear to operate in favor of a certain detention of *Eciton* males in their colony of origin.

We have seen that, within the first nights after the main part of a male brood has emerged from cocoons, the alates begin to appear outside the bivouac in limited numbers. A few of them at a given time may be seen in action on the surface close to the bivouac, alternately engaged in short spurts of running or (more frequently on further nights) in bursts of wasplike wing-vibration and in clumsy short flights. The way in which each active male is closely followed and actually gripped by workers may serve as a deterrent to premature departure flights. Another factor which would appear to retard the depletion of a brood of alate males is their involvement in the bivouac-change exodus. Most of them, when they leave the bivouac, pass almost at once into a directionalized stream of workers, and once in the column they make their way more or less directly to the new home site. Seldom are they free to run or flit about and to mount low vegetation (that is, to enter the pre-flight condition) except on rare occasions as when a major traffic interruption occurs (e. g., crossing of the route by a night-raiding hypogaecic *Eciton*). The new bivouac is entered directly by most of them, with little opportunity to stray.

The result is that probably not more than a few dozen or at most a few hundreds of the alates leave the colony on a given night, and hence the male brood is not entirely gone until three weeks or perhaps a longer time after its emergence from cocoons. Hence our findings confirm the hypothesis of M. R. Smith (1942) that *Eciton* males do not remain long in the parental bivouacs after emerging as callows. Since they fly off in greater numbers on moonlight nights, it may be that the males are all away sooner when a brood emerges during a period of full moon. The fact that male broods leave the colony in nightly lots inevitably increases the chances that at least a few of the males may get into colonies of their own species. Within a period of three weeks it is reasonably certain that any "loaded" colony will

come within male-flight range of one or more conspecific colonies.

Preliminary ground activity appears to be prerequisite to flight. Much excited running about and intermittent bursts of wing action are regular preliminaries to the take-off flight of *Eciton* males. In the case of any given male such behavior may last as long as thirty minutes before he actually flies away. We have mentioned the possibility that the retinue of workers may function incidentally to prevent premature flights. The existence of an organic build-up process of given duration is suggested by the fact that, up to the moment of actual departure, there appears to be little actual flying other than occasional short hopping flights.

Evidently, the take-off generally involves a clear departure from the vicinity of the home colony. Some of our results indicate that the flights carry over distances of at least a few hundred meters from the parent colony. Thus it may be possible for an *Eciton* colony to distribute males widely through a fairly large area around each bivouac site occupied during the period when nightly flights are being made by males. The process of dispersion must be assisted considerably by the influence of air currents and wind. Furthermore, the area which can be "seeded" with males from a given colony is greatly augmented through the fact that from the time the male alates first emerge their colony is nomadic; i. e., through about 12 days in *E. burchelli* and 17 days in *E. hamatum*. This of course means that each night finds the colony in a new focus of distribution relatively distant from the preceding site. These positive factors operate against numerous hazards of the flight which must tend to reduce greatly the chances that any given male will survive and eventually reach a scene of possible reproductive function. For, as we shall see, flight (or its equivalent) and dealation appear to be prerequisites for sexual response and function in *Eciton* males.

In view of the fact that a male *Eciton* brood probably contains a minimum of two or three thousand individuals as a rule, and that dozens or even hundreds of alates may leave a loaded colony on a given night, we are impressed by the rarity with which dealate males are observed in association with colonies. In contrast to the great frequency with which *Eciton* males (of hypogaecic species) are taken at lights, a survey of the doryline literature shows that dealate males are found only exceptionally.

The first discovery of this kind on record occurred in western Africa near the Gaboon R., in April of 1847, when Savage (1849) observed a few large insects later identified as dealated males of *Dorylus nigricans*, running back and forth in the columns of a colony of this species. These dealates were able to return and were readily accepted by the workers when displaced from the route. The first *Eciton* male dependably referred to its species was a male with only remnants of wings taken by W. Müller (1886) on

March 1, 1885, from a column of *E. burckhelli*. The ants evidently were engaged in a bivouac-change movement in which the male was participating, for Müller noted that his find was partially running and partially nudged along by workers. On October 21, 1905, K. Fiebrig took a single dealate male from a column (also evidently migratory) of *E. (Lab.) praedator* in San Bernardino, Paraguay (Forel, 1906). Reichen-sperger (1926) reported a "developed" male and single queen of *E. (E.) mattogrossensis* present to him in 1924 from Monte Alegre, Pará, after having been captured from the nest of the same colony. The finder, P. Cherubim Mones O. F. M., judged that a migration was in progress at the time. On November 29, 1911, Wheeler (1912) took two winged males of *E. (E.) vagans* near San Jose, Costa Rica, in a column of workers. Since these last males were taken in the daytime and evidently from raiding columns, presumably they were recent post-flight individuals. From a long file of *E. (Acam.) pilosum beebei* at Kartabo, British Guiana, in July of 1920 Beebe took two partially dealated males, and a little later on the same day Wheeler (1921) removed two additional males from the same column in which they "were being conducted along by the workers." Smith (1942) reported that D. E. Read found three dealate males in a nest of *E. (Acam.) carolinense* which was excavated in the vicinity of Spartanburg, S. Car.

My own experiences, based upon a concerted searching of Eciton bivouacs, further suggest that very few Eciton males reach colonies after their flights. In the first place, their seasonal occurrence is indicated by the fact that despite countless chances for discovery, only one dealate male has come to light during four rainy season surveys.¹¹ Further, in more than twenty Eciton colonies which were examined by me in southern Mexico during several months of the regular dry season of 1945, only one dealate male was found in any of the bivouacs. This male was found on May 1, 1945, in the midst of a mainly subterranean *E. hamatum* bivouac in a dry forest in northeastern Oaxaca (Schneirla, 1947). Relatively few dealate males were found in the present study.

It seems very probable that under ordinary conditions most of the few thousand alates in a given Eciton male brood are lost through the flight, and that only a small handful of them succeeds in getting into colonies. The possibility must also be considered that some of those which reach colonies of their species may be killed by work-

ers when first encountered on raiding trails or in other ways may have their span of life cut short after entering the bivouacs. It is probable that the greatest part of the male output is lost after landing from the flight, through the action of hazards such as predators, exposure and desiccation.

It is apparent from our evidence that very few of the males re-enter their own parental colonies, confirming the surmise of Gallardo (1920) that the flight operates against inbreeding and in favor of cross-fertilization.

Evidently the males can get into other colonies only by chance after their flight through happening to cross chemical trails in the course of their running about. Observations and appropriate tests show that Eciton males can follow the chemical trails of other colonies of their species. Hence, among those males that survive for any length of time after the flight, the ones that happen to encounter a chemical trail of their own species while wandering about on the ground may thereby reach a bivouac. (This wandering process is of course inferentially inserted here, since Eciton males have not been captured, either as alates or dealates, on the ground except with columns of workers or in bivouacs.) The process of such trail discovery, if it actually occurs, must be highly fortuitous. For example, the trail would have to be crossed near a bivouac or the male might get lost in its ramifications, must be a recent one or it might be too faint to be followed, and so on. Casualties must be numerous.

It should be noted that the ability of males to follow chemical routes thus encountered may be the outcome of a habituation to their own colony (and species) chemical during their initial stay of some days in the parent bivouacs. Also these chemical stimuli have been followed when the colony bivouac-change routes are travelled by the male callows during nightly bivouac-change movements. Furthermore, the pre-flight stay of males in their parent bivouacs may operate to insure the adequate impregnation of cuticular surfaces with the species chemical, thereby increasing the chances that in possible post-flight arrival at the trails of other colonies they will not be attacked by the foraging workers.

Since the males retain their wings through a rather lengthy stay in their parent colony, and since we find them without wings relatively soon after the flight, it would appear that through the flight itself physiological changes are set up which lead to dealation. The process may resemble the characteristic post-flight dealation of queens which prevails widely among most species in ant subfamilies other than the dorylines. The matter deserves special study.

It may be that the flight is essential for the occurrence of mating behavior and reproductive function in the Eciton male. The Ecitons exhibit the predominant tendency among ants for a full male flight under ordinary natural conditions.¹² However, at

¹¹ On June 13, 1932, in the early weeks of the rainy period, a single dealate male was found running in a column of *E. hamatum* workers. The male was in the last section of a bivouac-change movement which had been delayed by rain and was completed shortly after the find, at 9:00 a.m. He ran under his own power, although occasionally the workers which crowded closely around and after him nipped and tugged at his legs when he paused or started to reverse directions. This was the only dealate male observed in three periods on Barro Colorado Island in the early months of rain, when, presumably, dealate males might still be present in some of the colonies.

present we do not know whether under any conditions the males may go flightless without impeding their eventual fertility. In the present investigation a few tests of preliminary nature were made in which alate *Eciton* males were found not especially responsive to queens. But on the other hand in just two opportunities to test the behavior of dealates placed together with queens, coupling occurred within a period of minutes. Gallardo (1920) considered it unlikely for hypothetical reasons that fertilization may be carried out by *Eciton* males that have not made their flight. He observed that males of *E. (Lab.) praedator* taken at lights by E. Caride had the genital organs completely distended, a condition noted also by the present writer in the case of *E. (Lab.) coecum* males taken around lights at Barro Colorado in May of 1933. It is barely possible that the flight itself may set up physiological changes prerequisite to mating, as Goetsch (1933) has suggested for termites. However, in certain termites Grassé (1942) has obtained dealation and successful mating through isolation without benefit of any flight, and C. P. Haskins (personal communication) has obtained comparable results with the alates of certain ponerine ant species.

By and large, male flight appears to be the rule among the *Ecitons*, presumably insuring a predominance of cross-fertilization of apterous young queens in foreign colonies. However, we must reserve the possibility that on occasion short flights or the activity-equivalent of flight may permit a return into the parental colony, and subsequent inbreeding.

Finally, let us consider whether our findings cast any light on the problem of when, how, and by what individual or individuals the male eggs are produced. The last question would seem to have priority. If the Dzierzon rule holds for *Ecitons* as it holds widely among other social insects (Phillips, 1915; Snodgrass, 1925), then army-ant males arise from unfertilized eggs which might be laid by workers or by a regular queen. Of course workers as possible male-producers cannot be excluded without good reason, since production of males from worker eggs has been demonstrated in numerous species of bees (Plath, 1922; Snodgrass, 1925), is known to be common among ant species particularly when colonies are old and well-fed (Fiedle, 1905; Emery, 1918; Wheeler, 1928; Weyer, 1929), and is even believed by Verlaine (1926) to be virtually the rule among social insects. In fact, Haskins and Enzmann (1945) have reported evidence that in certain ponerine species not only males but also females may arise

from impaternal worker eggs. Worker ants of many species are known to possess ovarioles (Bickford, 1895; Holliday, 1904), although in virtually all investigated cases workers have fewer than in the queen. Mukerji (1933) discovered ovaries in two of twelve workers of the Old World species *Dorylus (Alaopone) orientalis* examined by him, with indications that one of these workers might have been capable of producing eggs. At present evidence is lacking that the workers of New World doryline species may be functional. The anatomical evidence is meagre and negative, since Miss Holliday found no evidence of ovarioles in several workers of *E. (Acam.) schmitti* which she studied histologically.

The findings reported in this paper flatly oppose the possibility that in *Eciton (Eciton)* species male broods result from worker eggs. These broods number in the few thousands, and in our experience always appear as distinct all-male broods in which all individuals are approximately of the same age. There are far too many eggs in such broods, far too similar in time of production, to be conceivably the product of workers. A sporadic egg-production in small lots but not in precise broods, would be expected of workers. Moreover, such broods are always found to be exactly synchronized with other (worker) broods just as would be expected were the egg-laying cycle of a single colony queen responsible for all (Schneirla, 1944). In many laboratory observations of *hamatum* and *burchelli* workers in lots varying from a few dozens to a few hundreds, housed in artificial nests and given all possible care as to food and moisture in particular, the writer has found no evidence that eggs were ever laid. Contrary to the state of affairs existing rather widely among other ants, it is exceedingly doubtful that *Eciton* workers play any direct role in species genetics by functioning as reproductives.

We have concluded that *Eciton* male-production is a seasonally-conditioned process, limited (at least in the area and under the conditions of this study) to the dry season. From our previous evidence (Schneirla, 1944; 1947), the *Eciton* colony queen at regular intervals throughout the year produces huge batches of inseminated (i. e., functionally diploid) eggs, resulting in successive large worker broods through the rainy season and most of the dry season. In the present investigation we have found that during the early part of the dry season there arises somehow as a regular delivery episode in the given queen's cycle a much smaller batch (and probably only one) of male-producing eggs.¹³

On the Dzierzon rule these eggs which produce males are presumably unfertilized, functionally haploid eggs. What can account for this seasonally-conditioned and time-limited change in the queen's function? It might be thought that these eggs are laid

¹² Whether or not a flight is indispensable, pre-nuptial flying evidently occurs in the males of all ant subfamilies, except for the minority of species in which the male lacks wings (e.g., certain species of *Ponera* and *Cardiocondyla*—Wheeler, 1913). Thus the males went aloft in all four of the myrmecine and camponotine species investigated by Talbot (1945). In these same species female flight also appeared to precede mating, although it was limited mainly to wing action on the ground in the bulky females of *Preloplepis imparis*.

¹³ How young queens are produced in *Eciton* colonies is unknown at present.

by old queens whose sperm supply is exhausted. Male-production by old queens is known to occur in honeybees, and Goetsch (1939) has reported it for certain ants. However, it is very doubtful that this can be the regular mode of male-production in the Ecitons. We have found several male broods in *E. burchelli* and *hamatum* which were followed (and some of them known to have been preceded) by regularly-spaced worker broods. Although the writer has a little (unpublished) evidence for the possible refertilization of functional colony queens in *E. hamatum*, there is no good reason to believe that such events occur widely as sequels to an annual exhaustion of sperm accounting for male broods. In the absence of direct evidence, it seems wiser to hypothecate a temporary process of blocked insemination of eggs by virtue of seasonal and time-limited causes.

The possibility that at given times the effective fertilization of eggs by sperm is prevented temporarily through a reflex-physiological change in the queen has been made plausible by the recent studies of Flanders (1946) on the honeybee and by earlier work on other insects. Flanders finds significant evidence justifying the idea long known as the "Wagner theory" (cf. Phillips, 1915, p. 188). In the queen honeybee it is probable that under certain conditions of extrinsic stimulation (e. g., small comb cells) the sperm valve may open, permitting the release of sperm from the spermatheca and the fertilization of eggs; whereas under other stimulative conditions (large cells; old comb) the valve remains closed and unfertilized male eggs are laid. In the fertile females of other insects, equivalent stimulative conditions may control fertilization in a corresponding manner (see Flanders, 1939). The seasonal production of males with species differences in the timing is an occurrence widely present among ants (Talbot, 1945), and male-producing eggs are commonly laid in the autumn by honeybee queens (Vandel, 1930). Insects in general are known to be rather delicately affected metabolically by changes in environmental conditions such as prevalent temperature and humidity (Uvarov, 1931; Chapman, 1931; Buxton, 1932; Himmer, 1932; Mellanby, 1935). Their reproductive processes are known to be affected by ecological conditions (Alpatov, 1932; Wigglesworth, 1934). Since, as Ezikow (1926) and others (Wheeler, 1913) have shown, the ovaries of queen ants react in a fairly sensitive manner to the prevailing metabolic condition of the individual, it is conceivable that a delicately adjusted process such as that which must underlie the impressive egg-production rhythm of the Eciton queen might be affected temporarily by an abrupt change in general conditions. A reasonable hypothesis would appear to be that seasonally the Eciton queen is so influenced by the first impact of dry-season conditions that the fertilization process is temporarily blocked. Despite the occurrence of a vertical

shifting of Eciton bivouac sites in dry terrain (Schneirla, 1947) which may act as a partial buffer for the queen against non-optimal atmospheric conditions, it is possible that a time lag may exist in the queen's readjustment to these or related seasonal changes (such as available water in food,—Buxton, 1932) sufficient to account for a temporary inhibition of insemination. While these considerations may seem reasonable, they must be regarded as highly tentative in the absence of direct evidence concerning the ecological relationships of Eciton reproductive processes.

RÉSUMÉ AND CONCLUSIONS.

Males of the two investigated species of *Eciton* (*Eciton*) appear during the first half of the regular dry season, in distinctive broods of about 3,000 individuals each. Male-production in the 1946 season began a few weeks earlier in *E. burchelli* than in *E. hamatum*.

The production of one male brood per colony in a given season appears to be the rule, with some colonies having none. Results indicate that the male brood is the progeny of the regular colony queen, since it appears that the all-male brood of a given colony generally arises as a regularly synchronized episode in the reproductive cycle, spaced between worker broods.

It is suggested that the impact of dry-season conditions operates to inhibit the insemination process of the queen completely so that a batch of male-producing unfertilized eggs is laid before a readjustment to dry-season conditions somehow occurs.

Results show that a male brood has trophallactic stimulative relationships with workers comparable to those ordinarily exerted by a worker brood. Once larval development is well under way, the energizing effect of a male brood is comparable to that exerted by a worker brood roughly ten times its population size. Since male developmental phases are largely the same as those of worker broods, the appearance of male broods occasions no substantial modification of the (nomad-statary) cycle of colony behavior changes.

The complete dissemination of alate males from the parental colony begins a few nights after emergence and ordinarily requires about three weeks for its completion. The alates escape in nightly lots, which perhaps are larger on moonlight nights than at other times. The expenditure of a given brood of alates in flight may be retarded both through the behavior of workers and through participation of males in bivouac-change movements.

The male flight operates largely in favor of cross-breeding of colonies, although inbreeding evidently is not excluded. The "seeding" of males from a given colony is widened greatly in scope by the fact that (in the species studied and probably also in others) colonies are nomadic for a number of days after the alates emerge.

Most of the alate males evidently are lost through the flight, and few reach a situation of possible reproductive function. It is suggested that upon landing after the flight, males generally get into other colonies through chancing upon and following the chemical trails established in the daily colony raids. The pre-flight stay of alates in their parental colonies may operate to prepare them for this process, by habituating them to species chemical as in trail-following, and by insuring the saturation of their cuticle with species chemical. Thus acceptance of males into other colonies of their species may be facilitated through the chemically conditioned responses of workers to them much as to nestmates rather than as to booty.

BIBLIOGRAPHY.

- ALPATOV, W.
1932. Egg production in *Drosophila melanogaster* and some factors which influence it. *Journ. Exper. Zool.*, **63**: 85-111.
- BEEBE, W.
1919. The home town of the army ants. *Atlant. Mo.*, **124**: 454-464.
- BICKFORD, E. E.
1895. Über die Morphologie und Physiologie der Ovarien der Ameisen-Arbeiterinnen. *Zool. Jahrb., Syst.*, **9**: 1-26.
- BRAUNS, J.
1901. Ueber die Lebensweise von *Dorylus* und *Aenictus*. *Zeitschr. syst. Hymen. Dipt.*, **1**: 14-17.
- BRUCH, C.
1916. Contribución al estudio de las hormigas de la provincia de San Luis. *Rivist. Mus. La Plata*, **23** (2): 291-357.
1924. Descripción de la reina "*Eciton* (*Acamatus*) *hetschkoii*" Mayr. *Physis*, **7**: 232-235.
- BUXTON, P. A.
1932. Terrestrial insects and the humidity of the environment. *Biol. Rev.*, **7**: 275-320.
- CHAPMAN, R. N.
1931. Animal Ecology with especial reference to Insects. New York: McGraw-Hill Book Co.
- EMERY, C.
1895. Le problème des *Dorylus*. *Bull. Soc. ent. France*, 1895.
1918. Esperienze intorno alla produzione di individui sessuati nella società delle Formiche. *Rend. R. Accad. Sci. Inst. Bologna, Cl. Sci.*, **22**: 65-72.
- EZIKOV, J.
1926. Über den Character der Variabilität der Ameisen-Ovarien. *Rev. Zool. Russe*, **3**: 333-356.
- FIELDE, A.
1905. Observations on the progeny of virgin ants. *Biol. Bull.*, **9**: 355-360.
- FLANDERS, S. E.
1939. Environmental control of sex in hymenopterous insects. *Ann. Ent. Soc. Amer.*, **32**: 11-26.
1946. Control of sex and sex-limited polymorphism in the Hymenoptera. *Quart. Rev. Biol.*, **21**: 135-143.
- FOREL, A.
1906. Fourmis neotropiques nouvelles ou peu connues. *Ann. Soc. Ent. Belgique*, **50**: 225-249.
- GALLARDO, A.
1915. Observaciones sobre algunas hormigas de la Republica Argentina. *Ann. Mus. Nac. Hist. Nat. Buenos Aires*, **27**: 1-35.
1920. Las hormigas de la Republica Argentina—Subfamilia dorylinas. *Ann. Mus. Nac. Buenos Aires*, **30**: 281-410.
- GOETSCH, W.
1933. Die chilenischen Termiten. *Zool. Jahrb., Syst.*, **64**: 227-244.
1940. Vergleichende Biologie der Insekten Staaten. Leipzig.
- GRASSÉ, PIERRE-P.
1942. L'essaimage des termites. *Bull. Biol. France Belgique*, **76**, Fasc. 4: 347-382.
- HARE, L.
1934. Caste determination and differentiation with special reference to the genus *Reticulitermes* (Isoptera). *Journ. Morph.*, **56** (2): 267-293.
- HASKINS, C. P. and ENZMANN, ERNST V.
1945. On the occurrence of impaternate females in the Formicidae. *Journ. N. Y. Ent. Soc.* **53**: 263-277.
- HAYDAK, M. H.
1943. Larval food and development of castes in the honeybee. *Journ. Econ. Ent.*, **36**: 778-792.
- HIMMER, A.
1932. Die Temperaturverhältnisse bei den sozialen Hymenopteren. *Biol. Rev.*, **7**: 224-253.
- HOLLIDAY, MARGARET
1904. A study of some ergatogynic ants. *Zool. Jb., Syst.*, **19**: 292-328.
- IHERING, H. VON
1912. Biologie und Verbreitung der brasilianischen Arten von *Eciton*. *Entom. Mitteilungen*, **1** (8): 226-235.
- LUEDERWALDT, H.
1918. Notas myrmecologicas. *Rev. Mus. Paulista*, **10**: 31-64.
1926. Observacoes biologicas sobre Formigas brasileiras. *Rev. Mus. Paulista (São Paulo)*, **14**: 185-304. 5 pl.
- LUTZ, F. E.
1929. Observations on leaf-cutting ants. *Amer. Mus. Nov.*, (388): 1-21.
- MAYR, G.
1886. Ueber *Eciton*—*Labidus*. *Wiener Ent. Zeitschr.*, **5**: 33-36.

- ELLANBY, K.
1935. The evaporation of water from insects. *Biol. Rev.*, **10**: 317-333.
- LUKERJEE, D.
1926. Digestive and reproductive systems of the male ant, *Dorylus labiatus* Schuck. *Journ. Proc. Asiatic Soc. Bengal*, **22**: 87-91.
- LUKERJI, D.
1933. On the anatomy of the worker of the ant *Dorylus (Alaopone) orientalis* Westw. *Zool. Anz.*, **105**: 97-105.
- MÜLLER, W.
1886. Beobachtungen an Wanderameisen. *Kosmos*, **18**: 81-93.
- PHILLIPS, E. F.
1915. Beekeeping. (Rural Science Series).
- PLATH, O. E.
1922. Notes on *Psithyrus*, with records of two new American hosts. *Biol. Bull.*, **43**: 23-44.
- REICHENSPERGER, A.
1926. Das ♀ von *Eciton mattogrossensis* Luederw. *Ent. Mitteil.*, **15**: 401-404.
1934. Beitrag zur Kenntnis von *Eciton lucanoides* Em. *Zool. Anz.*, **106**: 240-245.
- SANTSCHI, F.
1908. Nouvelles fourmis de l'Afrique du Nord (Égypte, Canaries, Tunisie). *Ann. Soc. Ent. France*, **77**: 517-534.
- SAVAGE, T. S.
1849. The driver ants of Western Africa. *Proc. Acad. Nat. Sci. Phila.*, **4**: 195-200.
- SCHNEIRLA, T. C.
1933. Studies on army ants in Panama. *Journ. Comp. Psychol.*, **15**: 267-300.
1934. Raiding and other outstanding phenomena in the behavior of army ants. *Proc. Nat. Acad. Sci.*, **20**: 316-321.
1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. *Journ. Comp. Psychol.*, **25**: 51-90.
1941. Social organization in insects, as related to individual function. *Psychol. Rev.*, **48** (6): 465-486.
1944. The reproductive functions of the army-ant queen as pacemakers of the group behavior pattern. *Journ. N. Y. Ent. Soc.*, **52**: 153-192.
1945. The army-ant behavior pattern: nomad-statory relations in the swarmers and the problem of migration. *Biol. Bull.*, **88**: 166-193.
1947. A study of army-ant life and behavior under dry-season conditions with special reference to reproductive functions. I. Southern Mexico. *Amer. Mus. Novitates*, (1336): 1-20.
- MITH, M. R.
1927. A contribution to the biology and distribution of one of the legionary ants, *Eciton schmitti* Emery. *Ann. Ent. Soc. Amer.*, **20**: 401-404.
1942. The legionary ants of the United States belonging to *Eciton* subgenus *Neivamyrmex* Borgmeier. *Amer. Midl. Nat.*, **27**: 537-590.
- SNODGRASS, R. E.
1925. Anatomy and Physiology of the Honey-bee. New York: McGraw-Hill Book Co.; 1-327.
- SUMICHRIST, F.
1868. Notes on the habits of certain Mexican Hymenoptera presented to the American Entomological Society. *Trans. Amer. Ent. Soc.*, **2**: 39-44.
- TALBOT, MARY
1945. A comparison of flights of four species of ants. *Amer. Midl. Nat.*, **34**: 504-510.
- UVAROV, B. P.
1931. Insects and climate. *Trans. Ent. Soc. Lond.*, **79**, pt. 1.
- VANDEL, A.
1931. La parthénogénèse. *Encycl. Scientifique, Paris*, 1931.
- VERLAINE, L.
1926. Les reines fécondées des Hyménoptères sociaux peuvent-elles normalement engendrer des mâles? *Ann. Bull. Soc. Ent. Belgique*, **66** (8/10): 287-318.
- VOSSELER, J.
1905. Die ostafrikanische Treiberameise (Siafu). *Pflanzer*, **1** (19): 289-302.
- WESSON, L. G.
1940. An experimental study of caste determination in ants. *Psyche*, **45**: 105-111.
- WEYER, F.
1929. Die Eiablage bei *Formica rufa* Arbeiterinnen. *Zool. Anz.*, **84** (9/10): 253-256.
- WHEELER, W. M.
1900. The female of *Eciton sumichrasti* Norton, with some notes on the habits of Texas Ecitons. *Amer. Nat.*, **34**: 563-574.
1912. The male of *Eciton vagans* Oliver. *Psyche*, **19**: 206-207.
1913. Ants—their Structure, Development and Behavior. New York: Columbia Univ. Pr.: 1-663.
1921. Observations on army ants in British Guiana. *Proc. Amer. Acad. Arts Sci.*, **56**: 291-328.
1928. The Social Insects. New York: Harcourt, Brace.
- WHEELER, W. and LONG, W. H.
1901. The males of some Texas Ecitons. *Amer. Nat.*, **35**: 157-173.
- WIGGLESWORTH, V. B.
1934. Insect physiology. London: Methuen, 1-134.
- WROUGHTON, R. C.
1892. Our ants. *Journ. Bombay Nat. Hist. Soc.*, **7**, Pt. I; 13-60; Pt. II: 175-203.

EXPLANATION OF THE PLATE

PLATE I.

Representative growth stages in males of
Eciton burchelli.

- Fig. 1. Larvae from the brood of colony B-I, taken at four-day intervals (cf. Text-fig. 1). Left, sample of March 2 (range of lengths, 5.6-6.6 mm.); middle, March 6 (range of lengths, 18.3-20.4 mm.); right, March 10, at larval maturity (range of lengths 22-24.8 mm.).
- Fig. 2. Post-larval male specimens from the brood of colony B-I. Left, pre-pupa of March 14, removed from cocoon; middle, pupa of March 25, removed from cocoon; right, enclosed pupa of March 25.
- Fig. 3. Mature males of *E. burchelli*. Left, alate post-flight males, preserved a few minutes after flight in laboratory cage; right, dealate males, preserved several hours after laboratory flight and loss of wings.

All specimens twice natural size.



FIG. 1.



FIG. 2.

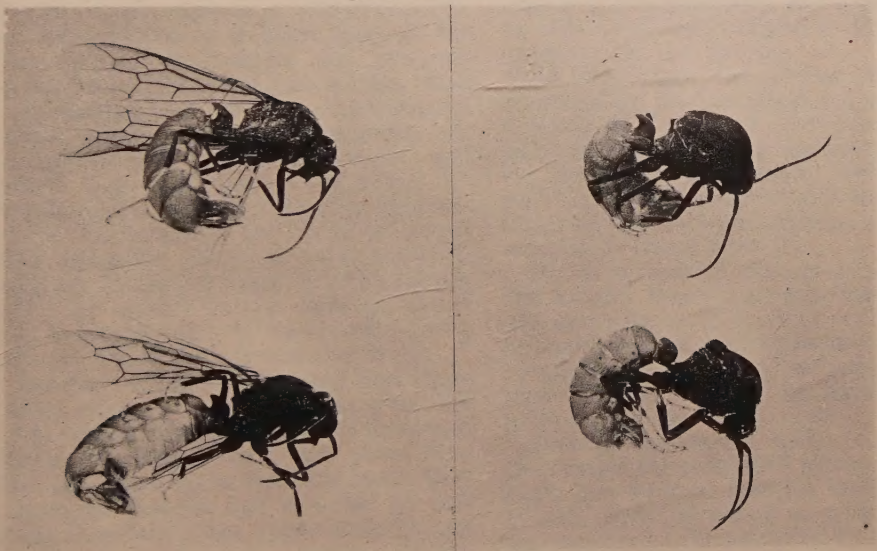


FIG. 3.

ARMY-ANT LIFE AND BEHAVIOR UNDER DRY-SEASON CONDITIONS WITH SPECIAL REFERENCE TO REPRODUCTIVE FUNCTIONS. II. THE APPEARANCE AND FATE OF THE MALES.

